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EXTRAFLORAL NECTAR FEEDING BY LADYBIRD BEETLES (COLEOPTERA: COCCINELLIDAE)

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Abstract.—Coccinellid beetles belonging to 41 species in 19 genera and 5 of the family's 6 coccinellid subfamilies were observed in the United States, China, Japan, and Korea, or are reported in the literature to feed on the extrafloral nectar of 32 plant species in 23 genera and 15 families. Extrafloral nectar feeding by coccinellids occurred throughout the world in diverse natural and man-made habitats. Since ladybird beetles are, at times, common and occasionally abundant visitors to extrafloral nectaries, they could reduce insect herbivores of the plants that bear the glands, much as do many extrafloral nectar feeding ants. Most extrafloral nectary feeding by ladybird beetles, however, was not observed in the presence of prey, nor usually where ants were abundant. Ladybird beetles were less frequent and less constant visitors to extrafloral nectaries than were ants, and appear by contrast to be poor mutualists to extrafloral nectary-bearing plants. Extrafloral nectar seems to be an important energy source for coccinellids in the absence of prey. It probably enhances ladybird beetle survival and may maintain them in the habitat, to feed on insect herbivores as they appear.

Key Words: Coleoptera, Coccinellidae, ladybird beetles, ants, extrafloral nectar, insect nutrition, plant defense

Extrafloral nectaries are secretory glands of plants usually located on the leaves, but also on the outer surfaces of reproductive parts (Bentley 1977a). Plants belonging to at least 93 families and of worldwide occurrence bear the glands (Zimmermann 1932, Elias 1983, Pemberton and Keeler unpublished data). During the past 25 years, numerous studies have demonstrated the role of ants that feed on extrafloral nectaries in reducing the insect herbivore damage to plants that bear the glands (Janzen 1966, Elias and Gelband 1975, Bentley 1977b, Tilman 1978, Keeler 1981a, Stephenson 1982, Pickett and Clark 1979). Predators other than ants and parasitoids are also frequent visitors to extrafloral nectaries (Springensguth 1935, Keeler 1978, Bugg et al. 1989). Many of these visitors probably cause increased mortality to the insect herbivores that feed on extrafloral nectary-bearing plants (Keeler 1978, Koptur 1985, Hespenheide 1985). In contrast to the many studies involving ants that feed on extrafloral nectar, the effects of non-ant predators and parasitoids that feed at the extrafloral nectaries are virtually unstudied. This undoubtedly reflects the difficulties in excluding predators and parasitoids without excluding the herbivores, most of which also fly (Beattie

1985). The ease with which walking ants can be excluded with resin barriers has contributed, in part, to the emphasis on ant studies.

The unknown and unmeasured benefits that non-ant predator and parasitoid extrafloral nectar feeders bring to the plants may explain (1) the occurrence of extrafloral nectaries in plants living in places like Hawaii, where there are no native ants (Keeler 1985) and (2) the maintenance of extrafloral nectaries in plant populations having ant associates that are ineffective protectors (O'Dowd and Catchpole 1983, Tempel 1983, Koptur and Lawton 1988).

Among predators that feed on extrafloral nectar are the adults of Coccinellidae. Springensguth (1935) observed these beetles feeding at the extrafloral nectaries of many plants in Germany. Coccinellids are more abundant in cotton cultivars that have extrafloral nectaries than in those lacking the glands (Schuster et al. 1976, Adjei-Maafo and Wilson 1983), and they are conspicuous visitors to the extrafloral nectaries on the leaves of peach in Ontario (Putnam 1963). Stephenson (1982) observed *Coccinella* spp. feeding on the extrafloral nectaries of *Catalpa speciosa* Warder and then attacking the eggs and first instar larvae of *Ceratomia catalpae* (Boisduval) (Sphingidae), the plant's primary herbivore.

The objectives of this study were (1) to learn what kinds of coccinellids use extrafloral nectar and from which types of plants and in what situations, and (2) to use these observations and records to consider the benefits of extrafloral nectar feeding to the coccinellids and the plants that bear the glands.

Materials and Methods

Most observations of coccinellids feeding at extrafloral nectaries were made from 1986 through 1990 during research on the occurrence of extrafloral nectary plants in California, Korea, and Montana (Pemberton 1988, 1990, unpublished data). To increase the chances of seeing coccinellid feeding, extrafloral nectaries were also frequently examined during visits to gardens, parks, and during unrelated field work in China, Japan, Korea and the U.S.A. A few plants were monitored frequently including: *Prunus laurocerasus* L., *Prunus serratula* Lindley and *Viburnum opulus* L. in Berkeley, California in 1987; *Prunus virginiana* L. and *Populus tremuloides* Michaux in Bozeman, Montana in 1988; and *Prunus padus* L. in Seoul, Korea in 1989, and *Azukia radiatus* (L.) in Yangsuri, Korea in 1990. Care was taken to actually observe feeding and not merely resting at the site of the nectary. After feeding was observed, the beetle was captured and identified. The field observations were made by the first author (RWP) and the coccinellids identified by the second author (NJV), except for Korean material, which was identified by H. C. Park and a Japanese scymnine identified by R. D. Gordon.

The literature was examined for records of coccinellids feeding on extrafloral nectar. These records were interpreted and are reported using current coccinellid classification and nomenclature.

Results and Discussion

Forty-one coccinellid species were recorded to feed on extrafloral nectar from our observations and from the literature (Table 1). These species belong to 19 genera and 5 of the world's 6 coccinellid subfamilies (Fürsch 1990). The greatest number of extrafloral nectar-feeding species (26 in 8 genera) belong to the Coccinellinae. The Chilocorinae had seven species in three genera, the Scymninae five species in three genera, the Epilachninae two (or more) in one genus and the Coccidulinae a single species. The many observations of Coccinellinae may relate to the ease with which these brightly colored lady beetles can be observed, as well as their relative abundance at extrafloral nectaries.

All records are of adults feeding at extrafloral nectaries, except for Geyer's (1947)

Table 1. Observations and literature records of extrafloral nectar feeding by coccinellid beetles.

Coccinellid Species	Extrafloral Nectary Bearing Plant	Extrafloral Nectary Site	Locality or Literature Record
Scymninae			
Cryptolaemus montrouzieri Mulsant	*Prunus laurocerasus* L. (Rosaceae)	leaf	Berkeley, Calif. (IV.19–21.87)
	Prunus persica (L.) (Rosaceae)	leaf	Berkeley, Calif. (VI.12.87)
Scymnus (*Pullus*) *japonicus* (Weise)	*Prunus padus* L. (Rosaceae)	leaf	Seoul, Korea (IV.5.89)
Scymnus (*Pullus*) sp.	*Prunus amygdalus* Batsch (Rosaceae)	leaf	Berkeley, Calif. (VI.12.87)
	Aleurities cordata R. Brown (Euphorbiaceae)	leaf	Tokyo, Japan (IX.16.86)
Stethorus punctillum Weise	*Prunus persica* (Rosaceae)	leaf	Missouri (Caldwell 1981)
		leaf	Ontario, Canada (Putnam 1963)
Stethorus sp.	*Prunus padus* (Rosaceae)	leaf	Seoul, Korea (IV.19.89)
Chilocorinae			
Brachiacantha ursina (F.) (as *Brachyacantha ursina* (F.))	*Prunus persica* (Rosaceae)	leaf	Missouri (Caldwell 1981)
Brachiacantha sp.	*Ipomoea carnea* Jacq. (Convolvulaceae)	leaf and/or flower stalk	Costa Rica (Keeler 1978)
Chilocorus cacti (L.)	*Chilopsis linearifolius* (Cavanilles) Sweet (Bignoniaceae)	flower bract	near Las Vegas, Nevada (V.21.87)
Chilocorus renipustulatus Scriba	*Prunus avium* L. (Rosaceae)	leaf	Germany (Springensguth 1935)
Chilocorus sp.	*Ailanthus altissima* Swingle (Simbariaceae)	leaf	Baltimore, Md. (IX.1988)
Exochomus flavipes Thunberg larvae	Cucurbitaceous plants	leaf	South Africa (Geyer 1947)
Exochomus quadripustulatus (L.)	*Prunus laurocerasus* (Rosaceae)	leaf	Berkeley, Calif. (IV.86)
Coccidulinae			
Rhyzobius lophanthae (Blaisdell)	*Prunus amygdalus* Batsch (Rosaceae)	leaf	Berkeley, Calif. (VI.18.87)
	Prunus laurocerasus (Rosaceae)	leaf	Berkeley, Calif. (VI.19–21.87)
Coccinellinae			
Hippodamia convergens Guerin	*Chilopsis linearifolius* (Bignoniaceae)	flower buds	Red Rock, Las Vegas, Nevada (V.30.87)
	Helianthus sp. (Compositae)	flower phyllaries	Texas (Rogers 1985)
	Opuntia echinocarpa Engelmann & Bigelow (Cactaceae)	areoles	Deep Canyon, Calif. (III.25.86)
	Prunus laurocerasus (Rosaceae)	leaf	Berkeley, Calif. (IV.19–21.87)
	Prunus persica	leaf	Missouri

Table 1. Continued.

Coccinellid Species	Extrafloral Nectary Bearing Plant	Extrafloral Nectary Site	Locality or Literature Record
	(Rosaceae)		(Caldwell 1981)
	Pteridium aquilinum (L.) Kuhn (Pteridaceae)	rachis	Tamales Bay, Calif. (IV.25.87)
	Vicia angustifolia Reichard (Fabaceae)	stipules	Placer Co., Calif. (VI.87)
	Yucca sp. (Liliaceae)	fruit	Cliff Dwellers, Arizona (V.26.87)
Hippodamia parenthesis (Say)	*Prunus persica* (Rosaceae)	leaf	Missouri (Caldwell 1981)
Hippodamia quinquesignata (Kirby)	*Populus tremuloides* Michx. (Salicaceae)	leaf	Bozeman, Mont. (V.12.88)
	Yucca glauca Nutt. (Liliaceae)	flower buds	Logan, Mont. (VI.19.88)
Hippodamia tredecimpunctata (L.)	*Prunus padus* (Rosaceae)	leaf	Germany (Springensguth 1935)
Hippodamia variegata (Goeze)	*Azukia radiatus* (L.) (Fabaceae)	flower stalk	Yangsuri, Korea (IX.20.90)
	Helianthus annuus L. (Compositae)	flower bracts and phyllaries	Seoul, Korea (VIII.1.89)
	Prunus avium (Rosaceae)	leaf	Germany (Springensguth 1935)
	Salix alba L. (Salicaceae)	leaf	Germany (Springensguth 1935)
	Serratula sp. (Compositae)	flower phyllaries	near Si Lin Houte, Inner Mongolia, China (VII.26.87)
Adalia bipunctata (L.)	*Helianthus annuus* (Compositae)	flower bracts and/or phyllaries	Germany (Springensguth 1935)
	Populus tremuloides (Salicaceae)	leaf	New York (Trelease 1881) Bozeman, Mont. (V.12.88)
	Prunus cerasus L. (Rosaceae)	leaf	Germany (Springensguth 1935)
	Prunus persica (Rosaceae)	leaf	Berkeley, Calif. (VI.12.87) Missouri (Caldwell 1981)
	Prunus virginiana L. (Rosaceae)	leaf	Bozeman, Mont. (V.5.88)
	Salix alba (Salicaceae)	leaf	Germany (Springensguth 1935)
	Sambucus nigra L. (Caprifoliaceae)	stipules	Germany (Springensguth 1935)
	Sambucus racemosa L. (Caprifoliaceae)	stipules	Bozeman, Mont. (V.13.88)
	Viburnum opulus L. (Caprifoliaceae)	leaf	Bozeman, Mont. (V.12.88)
	Vicia faba L. (Fabaceae)	stipules	Austria (Hetschko 1908)

Table 1. Continued.

Coccinellid Species	Extrafloral Nectary Bearing Plant	Extrafloral Nectary Site	Locality or Literature Record
	Vicia villosa Roth. (Fabaceae)	stipules	Germany (Springensguth 1935)
Coccinella novemnotata Herbst	*Helianthella uniflora* (Nutt.) Torr. & Gray (Compositae)	flower phyllaries	Bozeman, Mont. (VI.15.88)
	Yucca glauca (Liliaceae)	flower buds	Logan, Mont. (VI.19.88)
Coccinella quinquepunctata L.	*Centaurea jacea* L. (Compositae)	leaf	Germany (Springensguth 1935)
	Impatiens balsamina L. (Balsaminaceae)	leaf	Germany (Springensguth 1935)
	Prunus avium (Rosaceae)	leaf	Germany (Springensguth 1935)
	Vicia villosa (Fabaceae)	stipules	Germany (Springensguth 1935)
Coccinella septempunctata (L.)	*Centaurea jacea* (Compositae)	leaf	Germany (Springensguth 1935)
	Prunus avium (Rosaceae)	leaf	Germany (Springensguth 1935)
	Prunus cerasus (Rosaceae)	leaf	Germany (Springensguth 1935)
	Prunus spinosa (Rosaceae)	leaf	Germany (Springensguth 1935)
	Ricinus communis L. (Euphorbiaceae)	leaf and/or inflorescence	Germany (Springensguth 1935)
	Serratula sp. (Compositae)	flower phyllaries	near Si Lin Houte, Inner Mongolia, China (VII.26.87)
	Vicia cracca L. (Fabaceae)	stipules	Germany (Springensguth 1935)
(as *C. 7-punctata* L.)	*Vicia faba* L. (Fabaceae)	stipules	Austria (Hetschko 1908)
(as *C. 7-punctata* L.)	*Vicia sativa* L. (Fabaceae)	stipules	Austria (Hetschko 1908)
	Vicia sepium L. (Fabaceae)	stipules	Germany (Springensguth 1935)
Coccinella transversalis F.[a] (as *C. repanda* Thunberg)	*Gossypium* sp. (Malvaceae)	leaf and/or flower bracts	Australia (Adjei-Maafo and Wilson 1983)
Coccinella transversoguttata Faldermann	*Helianthella uniflora* (Compositae)	flower bracts	Bozeman, Mont. (VI.15.88)
	Populus tremuloides (Salicaceae)	leaf	Bozeman, Mont. (V.12.88)
	Prunus virginiana (Rosaceae)	leaf	Bozeman, Mont. (V.5.88)
	Sambucus raceomosa (Camprifoliaceae)	stipules	Hyalite Reservoir, Mont. (VI.18.88)
	Saussurea sp. (Compositae)	flower phyllaries	near Si Lin Houte, Inner Mongolia, China (VII.27.87)
	Yucca glauca (Liliaceae)	flower buds	Logan, Mont. (VI.19.88)

Table 1. Continued.

Coccinellid Species	Extrafloral Nectary Bearing Plant	Extrafloral Nectary Site	Locality or Literature Record
Coccinella trifasciata Mulsant	*Prunus laurocerasus* (Rosaceae)	leaf	Berkeley, Calif. (VI.12.87)
	Prunus persica (Rosaceae)	leaf	Berkeley, Calif. (VI.12.87)
Coccinella undecimpunctata L.[a]	*Gossypium* sp. (Malvaceae)	leaf and/or flower bracts	Egypt (Ibrahim 1955)
Coccinella sp.	*Prunus persica* (Rosaceae)	leaf	Missouri (Caldwell 1981)
Coccinula quatuordecimpustalata (L.) (as *Coccinella* 14-*pustulata* L.)	*Vicia faba* L. (Fabaceae)	stipules	Austria (Hetschko 1908)
	Vicia sativa L. (Fabaceae)	stipules	Austria (Hetschko 1908)
Coelophora inaequalis (F.)[a]	*Gossypium* sp. (Malvaceae)	leaf and/or flower bracts	Australia (Adjei-Maafo and Wilson 1983)
	Ricinus communis (Euphorbiaceae)	leaf and/or inflorescence	Hawaii (Nishida 1958)
Cycloneda munda Say (as *C. mundo* and *C. sanguinea* (L.))	*Prunus persica* (Rosaceae)	leaf	Missouri (Caldwell 1981)
Cycloneda polita Casey	*Prunus laurocerasus* (Rosaceae)	leaf	Berkeley, Calif. (VI.19–21.87)
	Prunus persica (Rosaceae)	leaf	Berkeley, Calif. (VI.18.87)
Cycloneda sanguinea (L.)	*Ipomoea carnea* (Convolvulaceae)	leaf and/or flower stalk	Costa Rica (Keeler 1978)
Harmonia axyridis (Pallas)	*Ailanthus altissima* (Simbariaceae)	leaf	Ming Tombs, Beijing, China (VII.10.87)
	Azukia radiatus L. (Fabaceae)	inflorescence	Yangsuri, Korea (IX.20.90)
adults and larvae	*Populus* sp. (Salicaceae)	leaf	Seoul, Korea (VII.19.89)
	Prunus persica (Rosaceae)	leaf	Beijing, China (VII.9.87)
	Prunus sp. (Rosaceae)	leaf	Yangsuri, Korea (IV.18.89)
	Sambucus sp. (Caprifoliaceae)	stipules	Yangsuri, Korea (IV.18.89)
Harmonia conformis (Boisduval)[a] (as *Leis conformis* Boisduval)	*Crotalaria striata* (*Fabaceae*)	flower stalk	Florida (Watson and Thompson 1933)
Harmonia octomaculata (F.)[a] (as *H. arcuata* (F.))	*Gossypium* sp. (Malvaceae)	leaf and/or flower bracts	Australia (Adjei-Maafo and Wilson 1983)
Micraspis frenata Erichson[a] (as *Verania freneta*)	*Gossypium* sp. (Malvaceae)	leaf and/or flower bracts	Australia (Adjei-Maafo and Wilson 1983)
Propylea japonica (Thunberg)	*Populus* sp. (Salicaceae)	leaf	Seoul, Korea (V.19.89)
Psyllobora vigintimaculata (Say)	*Prunus laurocerasus* (Rosaceae)	leaf	Berkeley, Calif. (IV.19–21.87)

Table 1. Continued.

Coccinellid Species	Extrafloral Nectary Bearing Plant	Extrafloral Nectary Site	Locality or Literature Record
	Prunus serrulata Lindley (Rosaceae)	leaf	Berkeley, Calif. (IV.22.87)
	Viburnum opulus (Caprifoliaceae)	leaf	Berkeley, Calif. (VI.2.87)
Subcoccinella viginti-quatuorpunctata (L.)	*Helianthus annuus* (Compositae)	flower phyllaries	Germany (Springensguth 1935)
	Prunus avium (Rosaceae)	leaf	Germany (Springensguth 1935)
	Pteridium aquilinum (Pteridaceae)	rachis	New Jersey (Tempel 1983)
	Viburnum opulus (Caprifoliaceae)	leaf	Germany (Springensguth 1935)
Epilachninae			
Epilachna spp.	*Ipomoea carnea* (Convolvulaceae)	leaf and/or flower stalk	Costa Rica (Keeler 1978)

[a] The reference implied but did not explicitly state that extrafloral nectar feeding occurred.

report of larval *Exochomus flavipes* Thunberg feeding on the glands of "curcurbits" in South Africa, and larvae of *Harmonia axyridis* (Pallas) feeding on the leaf glands of a hybrid *Populus* in Korea in 1989. In addition, an unidentified coccinellid larva was seen in 1988 feeding on the extrafloral nectaries of a quaking aspen (*Populus tremuloides*) planted in Washington, D.C. (Pemberton unpublished observation).

Coccinellids were observed to feed at the extrafloral nectaries of 32 plant species belonging to 23 genera and 15 families, in a total of 97 different coccinellid–plant associations. Plants bearing extrafloral nectaries were very diverse, ranging from a primitive fern (*Pteridium aquilinum* (L.) Kuhn) to advanced species of Compositae (*Helianthus* spp., etc.). Of the 18 coccinellid species that fed at the extrafloral nectaries of at least two plant species, 13 fed on those of plants belonging to two or more families. *Hippodamia convergens* Guerin fed on the extrafloral nectar of eight plants in seven families, and *Adalia bipunctata* (L.) used the extrafloral nectar of ten plants in five families. No specificity in coccinellid–extrafloral nectary plant associations was evident, although the beetles may well prefer some nectars over others.

There was a high incidence of feeding on the extrafloral nectaries of *Prunus* spp. (Rosaceae). Ten species of *Prunus,* including peach, cherry, and almond, were used by 24 of the 41 coccinellid species. *Prunus* extrafloral nectar feeding accounted for 35 of 97 coccinellid–plant associations. We suspect that the prominence of *Prunus* use relates to attention given this genus by the observers, as much as to the attractive qualities of its extrafloral nectar. Virtually all of the world's 430 *Prunus* species (Willis 1985) have extrafloral nectaries on the leaf petiole or leaf blade (unpublished data). *Prunus* species occur in most north temperate environments, and many species secrete large amounts of extrafloral nectar.

Coccinellid feeding on extrafloral nectaries occurred throughout most of the world, including Germany, Egypt, South Africa, Australia, China, Korea, Japan, Hawaii, North America, and Costa Rica. This behavior also occurred in a great diversity of environments and habitats such as deserts, grasslands, temperate deciduous and conifer forests, tropical dry forests, row-crop and orchard agriculture, and many urban situations. Rather than specializing on the extrafloral nectar of particular kinds of plants or environments, coccinellids appear to exploit available extrafloral nectar in the diverse environments they inhabit. *Hippodamia convergens* Guerin, for example, uses the extrafloral nectar of a cactus and a yucca in southwestern deserts, a fern in a moist Pacific Coast conifer forest, an ornamental *Prunus* shrub in urban Berkeley, California, and peach in Ontario orchards.

The coccinellids fed at extrafloral nectaries at various sites on the plants. Most glands were on leaf petioles and blades, but they also occurred on: stipules; flower stalks, buds, calyxes, phyllaries and bracts; fruits; the areoles or spine clusters of cacti; and the rachis (stem) branches of a fern.

Coccinellids fed on extrafloral nectar most frequently during April and May in California, April through August in Seoul, South Korea, and during May and June in Montana. These dates correspond to the periods in which extrafloral nectar is most readily available in these areas (Pemberton 1990, unpublished data). Secretion of extrafloral nectar is usually associated with new growth and often slows or ceases when leaves mature. Korea's rainy climate promotes new growth and active extrafloral nectaries throughout the summer, whereas the drier summers of central California and Montana limit new growth and most extrafloral nectary secretion to spring and early summer.

Most of the observations involved one or a few beetles. Most of the time that extrafloral nectaries were observed, coccinellids were not seen. This contrasts strongly with ants, which were frequently seen feeding at the glands of many plants. Due to the chanciness of seeing coccinellids actually feeding at extrafloral nectaries and the general uncommonness of such observations, quantitative data on the frequency of visitation were not collected, except for mung bean, *Azukia radiatus* (L.).

Of the plants monitored in Berkeley, *Prunus laurocerasus* (an ornamental, broad-leafed, evergreen shrub) commonly had coccinellids feeding at its foliar glands. Solitary adults of six species were observed at the glands for several weeks in April 1987. Nearby flowering cherries (*Prunus serratula*) were seen to have only one coccinellid visitor, *Psyllobora vigintimaculata* (Say), feeding at the leaf glands of one tree on one occasion, despite the copious amounts of extrafloral nectar produced by the leaves and the commonness of coccinellids in the environment. Similarly, fruit cherry trees (*Prunus avium* L.), growing in adjacent Albany, California, were not observed to have coccinellid visitors to their extrafloral nectaries. Many coccinellids, including *Adalia bipunctata,* which commonly feed on extrafloral nectar, were seen on these cherry trees feeding on aphids. Springensguth (1935) observed five coccinellid species feeding on cherry leaf extrafloral nectar in Germany. No coccinellids were seen on an ornamental "snowball" (*Viburnum opulus*) shrub for the first two months of observation, then in early June many *P. vigintimaculata* were seen feeding at the glands. *Prunus padus,* monitored in Seoul, Korea, had several *Scymnus japonicus* (Weise) feeding on the nectaries of its young leaves, daily for about two weeks in early April 1989, but not many afterwards. In Korea, the extrafloral nectaries on the inflorescences of 46 mung bean plants were observed (as a group) for two hours every week from September 20 through October 29, and then every four hours during a 24-hour period on September 20–21, 1990. Only two coccinellid individuals, one each of *Harmonia axyridis* and *Hippodamia variegata* (Goeze), were seen feeding at the extrafloral nectaries. They were on plants that had two and eight ants (*Formica fusca* L.), fewer ants than occurred on many other plants.

Only a few coccinellid species fed on extrafloral nectaries in large numbers. *Coccinella transversoguttata* Falderman fed in large numbers at the extrafloral nectaries on the newly opened leaves of quaking aspen, in Bozeman, Montana, for about one week in mid-May 1988. No aphids or other apparent food sources were present on the trees. Numerous *Harmonia axyridis* (Pallas) fed on extrafloral nectar from hybrid *Populus* leaf glands on the sucker growth and saplings growing along a canal in Seoul in mid-July 1989. Many *Hippodamia variegata* were seen feeding on nectar exuding from the outer surfaces of the flower head phyllaries of a *Serratula* sp., a thistle tribe member in the Compositae, on grasslands of Inner Mongolia, China in late July 1987. *Prunus virginiana* was observed to have *Adalia bipunctata* and *C. transversoguttata* frequently feeding on its leaf glands in early May 1988 in Bozeman, Montana.

Most coccinellids fed on extrafloral nectar where ants were either absent or less common than usual. Ant aggression was observed towards *Coccinella transversoguttata* when the beetles approached or fed at the glands of *Prunus virginiana* in Montana. The coccinellid ran away or pressed its body against the leaf or stem substrate. Aphid-tending ants have been observed to chase coccinellids from plants (McLain 1980) and have been thought to protect aphids from coccinellids (Nault and Montgomery 1976). The ant aggression exhibited towards coccinellids feeding at or approaching extrafloral nectaries may be analogous to ant protection of their homopteran honeydew resources.

Benefits to the coccinellids.—Studies on the composition of extrafloral nectar have shown that sucrose, glucose and fructose are the predominant solutes, but other sugars, amino acids, and miscellaneous organic compounds may be present in some species (Bentley 1977a). Many extrafloral nectars have all the 20 protein building amino acids, as well as a varying number of other amino acids (Baker et al. 1978, Pickett and Clark 1979, Rogers 1985, Caldwell and Gerhardt 1986).

The ten amino acids required for insect growth (Hagen et al. 1984) are usually found in extrafloral nectar. The primary benefit of feeding on extrafloral nectar appears to be the energy that sugars provide (Hagen 1962). If the amino acids were abundant enough, they could contribute to growth in coccinellid larvae and tissue maintenance in adults.

Extrafloral nectar may allow coccinellids to survive in the absence of prey (Hodek 1973). *Harmonia conformis* Boisduval (as *Leis conformis* Boisduval) uses extrafloral nectar when prey is scarce (Watson and Thompson 1933). *Coccinella undecimpunctata* (Reiche) is sustained on cotton extrafloral nectar in Egypt, during the summertime when normal foods are insufficient (Ibrahim 1955). Similarly, *Stethorus punctillum* Weise can survive for long periods on peach leaf nectar alone (Putnam 1963). Geyer (1947) increased adult longevity in *Exochomus flavipes* Thunberg from 8.6 days in the absence of food to 20.6 days with *Euphorbia ledienii* A. Berger floral nectar, which is probably nutritionally similar to extrafloral nectar.

Extrafloral nectar (and floral nectar) is probably nutritionally deficient for egg production or fat deposition (needed for egg production) (Hagen 1962). Prey or protein-rich artificial diets are nearly always necessary for egg development in predaceous ladybird beetles (Hodek 1973). *Stethorus punctillum* was unable to reproduce when fed only peach leaf nectar (Putnam 1963). The water component of extrafloral nectar could be valuable for coccinellids inhabiting deserts or other dry regions, particularly when insect prey is scarce or unavailable.

The abundance of extrafloral nectar food resources varies greatly in different plant communities. Reported percentages of cover occupied by extrafloral nectary-bearing plants include: 0.0% for four northern California communities (Keeler 1981); 0.0 to 28% for seven warm desert communities in southern California (Pemberton 1988); 7, 23, and 55% of three temperate deciduous forests in Korea (Pemberton 1990); and frequencies of 28 and 0.0% respectively for lowland and highland wet tropical communities in Jamaica (Keeler 1979).

Extrafloral nectar may well have been a food source for coccinellids since ancient times. Impressions of leaves with extrafloral nectaries and coccinellids have been found in the 35-million year old Florissant Formation of Colorado (Pemberton 1992).

Benefits to the plants.—Most (38 of 41) of the coccinellids observed to feed at extrafloral nectaries are predators of plant feeding arthropods, with various Homoptera being the most common prey. The others are two epilachinines (*Epilachna* spp.) that are plant feeders, and *Psyllobora vigintimaculata* (Say), a member of an unusual coccinelline tribe (Psylloborini) that feeds on powdery mildews (*Erisyphe* spp.). The following are summaries of the usual prey (Hodek 1973) for the coccinellid subfamilies with extrafloral nectary feeding species: Scymninae—phytophagous mites, coccids, whiteflies, mealybugs and other Homoptera; Chilocorinae—coccids, diaspine scales and aphids; Coccidulinae—coccids; Coccinellinae—aphids, also psyllids, whiteflies, coccids, immature chrysomelid beetles, and the plant pathogenic powdery mildews mentioned above for the Psylloborini; Epilachninae—phytophagous. Some coccinellids also feed on young instar larvae of Lepidoptera, Coleoptera, Hymenoptera, small nematocerous Diptera and Thysanoptera (Hodek 1973); all are prey groups in which plant feeders are dominant or common.

The ability of coccinellids to diminish the abundance of insect herbivores that feed on plants bearing extrafloral nectaries may be considerable. Whether predation is usually associated with extrafloral nectary feeding is unclear. Most of the coccinellid extrafloral nectar feeding observed in this study occurred where prey was not present or abundant. The benefit to plants may be a delayed effect. Coccinellids may be maintained on or near the plants, in the absence or scarcity of prey, by the extrafloral nectar resource. These coccinellids are then in a position to prey upon colonizing or outbreaking herbivores. *Coccinella undecimpunctata* adults, which fed on cotton extrafloral nectaries during the summer, were able to survive to produce a fall generation (Ibrahim 1955). *Coccinella transversoguttata,* which fed in large numbers at the extrafloral nectaries of quaking aspen in Montana (before aphids were apparent), were seen feeding on aphids on those same trees later in the season.

Most of our observations involved relatively few individuals seen once or only briefly. When larger numbers of coccinellids were seen feeding at the extrafloral nectaries of plants that were monitored over time (*Populus tremuloides, Prunus virginiana*), the feeding episodes were also brief. The pulses of large numbers of coccinellids feeding at the extrafloral nectaries could reduce important pests affecting the plants.

These observations suggest that coccinellid–extrafloral nectary associations are less predictable and constant than the relationships between many ants and extrafloral nectary bearing plants. Ants can be remarkably constant visitors to extrafloral nectaries, maintaining their presence throughout a plant's secretory period and regulating their densities according to the amount of nectar produced (Ruffner and Clark 1986). Korean *Formica fusca* were observed on the active extrafloral nectaries of mung bean 24 hours a day. On some plants (*Vicia angustifolia* Reichard in California), an assemblage of ant species provides a 24-hour presence at the extrafloral nectaries (unpublished data). Ants are often seen foraging at extrafloral nectaries in foggy or even rainy weather, whereas most coccinellids are usually active during the day in clear weather. Most ants have a stable and persistent presence in the habitats where they live, in contrast to coccinellids which are often quite transitory, either migrating or becoming dormant during part of the season. Most ants have a greater prey breadth than do coccinellids, many of which are specialized feeders. The predatory behavior of ants is often directly associated with extrafloral nectar feeding, which does not appear to be the case in coccinellids. In contrast to ants, coccinellids appear to be poor mutualists to plants that bear extrafloral nectaries.

One of the more interesting differences between coccinellid and ant visitors to extrafloral nectaries is their relationship to Homoptera. Many ants have mutualist interactions with Homoptera in which the ants protect aphids, scales, etc., for honeydew rewards (Way 1963). Homoptera are, as noted above, the primary prey of coccinellids. Extrafloral nectary plants particularly subject to homopteran attack could, in theory, benefit more from maintaining a coccinellid presence instead of ant-guards. The relative commonness of ants at extrafloral nectaries and their apparent protection of Homoptera from coccinellids probably precludes this kind of specialization for coccinellid-guards, even if coccinellids were more constant visitors. Not all ant species, however, can successfully protect aphids from coccinellid predation (McLain 1980). In addition, ants and coccinellids may be additive mortality factors of some insect herbivores, such as they are on the catalpa sphinx moth, the primary herbivore of the extrafloral nectary-bearing tree *Catalpa speciosa* (Stephenson 1982). Coccinellids may often contribute mortality that complements that of ants and other beneficial insects that feed on the extrafloral nectaries of plants.

The increased survival that extrafloral nectar feeding brings to coccinellids, coupled with the mobility of many lady beetles, probably results in increased coccinellid predation in the community of plants associated with extrafloral nectary-bearing species. Rogers (1985) suggested planting extrafloral nectary-bearing sunflowers in agricultural situations as a food source for nectar-feeding natural enemies (such as coccinellids). Planting sunflowers near crops, such as small grains, which are nectar poor, could increase the presence and feeding activities of natural enemies in the crops.

Gordon (1985) reported that 179 coccinellid species have been introduced to North America for biological control purposes. Most of these species have failed to establish. A better knowledge of coccinellid adult food sources, such as extrafloral nectar, and of the interactions between coccinellids and competing species such as ants, can assist in the colonization and management of these valuable insects.

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